

## Cotton Aphid (Homoptera: Aphididae) Abundance in Relation to Cotton Leaf Sugars

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Environ. Entomol. 33(3): 690-699 (2004)

**ABSTRACT** A 4-yr study (1997-2000) was conducted in the northern Texas Rolling Plains to determine whether the pyrethroid insecticide  $\lambda$ -cyhalothrin was associated with changes in nutritional quality (nonstructural carbohydrates, percentage leaf nitrogen and moisture, and total amino acids) of cotton leaves. Another objective was to determine the relationship between nonstructural carbohydrates (glucose, fructose, sucrose, and starch) in cotton leaves and change in cotton aphid, *Aphis gossypii* Glover, numbers during late summer and on formation of dark-colored morphs. Carbohydrate concentrations, percentage leaf moisture and nitrogen, and total amino acids were not significantly altered in cotton leaves by  $\lambda$ -cyhalothrin. Glucose, fructose, sucrose, sugar ratio [(glucose + fructose)/sucrose concentrations], leaf nitrogen, and moisture were significantly influenced by year and irrigation treatment. Regression analysis indicated that change in aphid numbers was influenced by numbers of aphids per leaf, temperature, leaf moisture and nitrogen, and sugar ratio. A negative linear relationship was observed between change in aphid numbers and sugar ratio; population growth was limited by high levels of glucose and fructose in cotton leaves, especially when temperatures were high and leaf moisture low. Percentage of dark-colored aphids was negatively correlated with temperature and daylength and positively correlated with leaf moisture and nitrogen and the sucrose/glucose ratio. Some of the nutritional and abiotic environmental variables that interact to regulate the occurrence of dark morphs are also interacting with other variables to influence the extent to which the reproductive potential will be expressed.

**KEY WORDS** cotton aphid, *Aphis gossypii*, cotton, leaf sugars, sucrose, glucose

SOME INSECTICIDES ARE KNOWN to induce outbreaks of the cotton aphid, *Aphis gossypii* Glover. For example, Kerns and Gaylor (1993) reported that cotton aphid numbers were higher in sulprofos-treated cotton compared with numbers in untreated cotton, and they suggested that sulprofos may have altered the biochemistry of the plant because concentrations of threonine and total essential amino acids were higher in the sulprofos-treated cotton. In another study, Kerns and Gaylor (1992) concluded that the rapid increase in aphid populations after sulprofos and cypermethrin was not a result of direct stimulation of aphid reproduction (hormologosis). Leser (1994) reported that rapid increases in aphid numbers were associated with applications of the pyrethroid insecticides bifenthrin, cyhalothrin, cypermethrin, and deltamethrin. Cotton aphid numbers increased within 2 wk of an application of cyhalothrin, and the increases did not seem to be caused by a reduction in predator populations (Kidd et al. 1996). In a laboratory study, Parajulee and Slosser (2001) found that net reproductive rate of

cotton aphids reared on cyhalothrin-treated leaves was significantly higher than for aphids reared on untreated cotton leaves, and they concluded that the increases were a result of indirect stimulation of reproduction (trophobiosis). All of these reports indicated that rapid increases of cotton aphids after application of some insecticides were not the result of destruction of natural enemies. Bartlett (1968) reviewed the influence of 59 insecticides on cotton aphids; he concluded that some of these probably did stimulate reproduction in cotton aphids and spider mites, and population increases were generally associated with persistent materials. Gordon and McEwen (1984) suggested that azinphosmethyl stimulated reproductive hormones in the green peach aphid, *Myzus persicae* (Sulzer).

Ravindhran and Xavier (1997) suggested that higher cotton aphid populations after pyrethroid applications were associated with increases in total sugars and decreases in phenol content in cotton leaves. However, in a study using cotton varieties with varying levels of resistance to cotton aphid, Liu and Yang (1993) reported that aphid suppression was associated with increased concentrations of soluble sugars in the leaves.

All aphid species that have been reared on artificial diets require sucrose (Srivastava 1987), but the opti-

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imum concentration varies with species. Auclair (1967a) reported that cotton aphids can tolerate large variations (10–40%) in sucrose concentrations in artificial diet but that a diet with 30% sucrose was about optimum for survival and reproduction, whereas survival was lower on diets with a 10–15% sucrose concentration. The optimum concentration of sucrose was 50% in diets for the turnip aphid, *Lipaphis erysimi* (Kaltenbach), but nymphs died when concentrations were  $\leq 15\%$  (Pant 1985). However, in feeding rate studies 10–20% sucrose was the best concentration for the green peach aphid (Mittler 1967). Although sucrose is generally acknowledged to be an important dietary component for aphids, the role of glucose, fructose, and other sugars is varied. Survival and reproduction of cotton aphids on diets containing 15% glucose or 15% glucose + 15% fructose was considerably lower than for aphids on diets containing 30% sucrose, and Auclair (1967b) concluded that glucose was detrimental to growth and survival. In feeding tests using various sugars, Weibull (1990) found that sucrose was the strongest phagostimulant for the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), whereas glucose was least preferred. However, Campbell et al. (1986) reported that the greenbug, *Schizaphis graminum* (Rondani); pea aphid, *Acyrtosiphon pisum* (Harris); and green peach aphid displayed positive feeding responses to glucose.

Explosive cotton aphid population increases are associated with a change in color from yellow to dark green. During midsummer cotton aphids are typically yellow and populations exhibit little tendency for increase. However, as the season progresses, there is a noticeable change to darker colored aphids. Wilhoit and Rosenheim (1993) reported that populations reached high levels only when some of the aphids were in the dark color form, and they found that aphids became darker as temperatures decreased late in the season. These workers also reported that fecundity increased after irrigation. In subsequent studies, Rosenheim et al. (1994) reported that induction of dark forms was associated with cool temperatures, short daylengths, and plants with high nitrogen content.

One objective of this study was to determine whether applications of a pyrethroid insecticide were associated with subsequent changes in the nutritional quality of cotton leaves. A second objective was to establish the relationship between soluble sugars (glucose, fructose, and sucrose) in cotton leaves and change in cotton aphid numbers during late summer and early fall and on formation of dark-colored aphid morphs.

## Materials and Methods

**Experimental Design.** This study was conducted over 4 yr (1997–2000) at the Texas Agricultural Experiment Station (Chillicothe, TX) (34° 12' N, 99° 32' W). 'TAMCOT Sphinx' was planted 2 May 1997, 30 April 1998, 28 April 1999, and 24 April 2000. Seeding rate varied between 17 and 19 seeds per meter of row

in 102-cm row spacings, and row direction was east-west. Fertilizer was applied at recommended rates immediately before planting at 33.6 kg N/ha in dryland plots and 67.2 kg N/ha in irrigated plots. Subplot size was 10 rows wide by 21.3 m in length. Irrigated and dryland plots were maintained in the same location all 4 yr, but chemical treatment subplots were randomly assigned each year.

A split-plot experiment arranged in a randomized complete block design was used, and treatments were replicated three times. Whole plot treatments were dryland, with no supplemental irrigation during the growing season, or irrigated, with last application in late August. Irrigation dates were 16 July, 7 and 29 August 1997; 24 April, 25 June, 16 and 29 July, 13 and 27 August 1998; 15 and 29 July, 12 and 27 August 1999; and 19 July, 7 and 25 August 2000. The dryland treatment was irrigated on 24 April 1998 to obtain sufficient soil moisture for planting. Plots were furrow-irrigated, and  $\approx 7$  cm of water was applied at each irrigation. The outside furrows in irrigated plots, adjacent to dryland plots, were not watered to prevent seepage across the rows.

Subplot treatments were an untreated check or an application of  $\lambda$ -cyhalothrin (Karate EC at 0.045 g [(AI)]/ha, Zeneca, Wilmington, DE) during anticipated periods of increased bollworm, *Helicoverpa zea* (Boddie), activity.  $\lambda$ -Cyhalothrin was applied on 29 July and 28 August 1997, 8 July and 12 August 1998, 2 and 25 August 1999, and 17 July and 24 August 2000. The water management and chemical treatments reported here represent a subset of the treatments reported previously by Slosser et al. (2001, 2002) who discussed the influence of these treatments on aphid populations and on sticky lint in cotton, respectively.

Chemicals were applied with a John Deere Hi-Cycle sprayer (Deere and Company, Moline, IL) with drops to provide three nozzles per row. Total solution applied varied between 101 and 109 liters/ha. The middle six rows within the 10-row plots were treated to minimize drift onto adjacent plots.

**Monitoring of Leaf Carbohydrate Profile.** Leaf discs were cut from cotton leaves for analysis of carbohydrates (glucose, fructose, sucrose, and starch) on the same dates that aphids were counted. Samples were taken once each week from untreated and  $\lambda$ -cyhalothrin-treated plots in dryland and irrigated treatments beginning in late July. A leaf from the fifth main stem node below the terminal was selected, and six discs, each measuring 0.33 cm<sup>2</sup> in area, were cut with a cork borer. Discs were cut from only one leaf per plot in 1997–1998, but samples were taken from two leaves per plot in 1999–2000. If the leaf was contaminated with aphids and honeydew, it was thoroughly washed with distilled water and blotted dry with paper towels before cutting the leaf discs. The six discs from each leaf were placed into 2 ml of an 80% ethyl alcohol solution in a stoppered test tube (13 by 100 mm) and placed immediately into a cool chest containing ice. Sampling was conducted between 9:00 AM and 12:00 PM. When sampling was completed, the test tubes

with leaf disc samples were stored in a freezer ( $-4^{\circ}\text{C}$ ) in the laboratory.

The leaf disc samples were sent to the USDA-ARS Western Cotton Research Laboratory (Phoenix, AZ) for carbohydrate analysis using the procedures of Hendrix and Peelen (1987) and Hendrix (1993). After removing the activated charcoal by centrifugation and filtration, a 200- $\mu\text{l}$  aliquot of the charcoal-treated supernatant was dried and analyzed by high-performance liquid chromatography (HPLC) by using the procedures given by Hendrix and Wei (1994). Hendrix (1993) outlined the method for determining starch in the ethanol-extracted residues. Starch was gelatinized with an amyloglucosidase mixture, and the clarified supernatant was analyzed by HPLC for glucose, by using glucose as a standard for the starch data. Total amino acids in the ethanolic leaf extracts were analyzed using the method of Stieger and Feller (1994) with alanine used as the standard.

**Leaf Moisture and Nitrogen.** Ten leaves from the fifth main stem node below the terminal were collected to determine leaf moisture on the same day that plots were sampled for leaf carbohydrate content. Leaves were pulled from the plants, and the 10 leaves from each plot were placed immediately into a plastic bag in an ice chest. Within an hour of being picked, leaf petioles were cut off with a sharp knife, and the leaves were weighed and then oven-dried at  $50^{\circ}\text{C}$  for 48 h. Percentage leaf moisture was calculated using the gravimetric method. When leaves were infested with aphids, the leaves were washed and thoroughly blotted dry with towels before weighing.

The leaves that were sampled for leaf moisture content after oven drying were then used to determine percentage leaf nitrogen. Total leaf nitrogen was determined on a dry matter basis using the Kjeldahl procedure (AOAC 1980) at the Texas Agricultural Experiment Station (Vernon, TX).

**Aphid Sampling.** Aphids were sampled once per week beginning late July in all 4 yr, and sampling continued until aphid populations peaked and then declined. Final samples were taken 22 September 1997, 8 September 1998, 13 October 1999, and 12 September 2000. Initially, aphids were counted on 10 leaves picked from the top and bottom half of the plant, for a total of 20 leaves sampled per plot, but sample size was reduced to five top-half and five bottom-half leaves when aphids exceeded  $\approx 100$  per leaf. Samples were taken from the middle six rows of a plot, and a leaf was picked every two to three steps along a row and visually examined for cotton aphids. Top- and bottom-half leaves were taken from different rows within a plot. Aphids were counted individually unless numbers exceeded  $\approx 100$  per leaf, when numbers were estimated by counting aphids in groups of five. A hand lens was frequently used during counting.

Before cutting the six leaf discs and leaf washing (see carbohydrate monitoring and leaf moisture and nitrogen sections above), the selected leaves were examined for aphids. Aphids were counted and classified as yellow morphs or dark (not yellow) morphs, and percentage of dark morphs was calculated.

**Climatic Data.** Temperature and rainfall data were obtained from the Texas Agricultural Experiment Station (Chillicothe). Solar radiation measurements were taken at the Texas Agricultural Experiment Station at Munday,  $\approx 81$  km south south east of the study fields at Chillicothe.

**Data Analyses.** Data were analyzed with analysis of variance (ANOVA), combined over years (McIntosh 1983), and by linear and stepwise regressions using Statistix 7 (Anonymous 2000). For ANOVA, main factors were year ( $n = 4$ ), irrigation treatment ( $n = 2$ ), chemical treatment ( $n = 2$ ), replication ( $n = 3$ ), and sample date, which was used as a repeated measure ( $n = 6$  for the data between 4 August and 12 September, 6 wk common to all 4 yr); at least one irrigation and one application of  $\lambda$ -cyhalothin were applied during that time frame.

Average change in aphid numbers per week was calculated as the difference between aphid numbers per leaf on two consecutive weeks, and the difference was divided by the number of days between weekly samples. Time varied between 5 and 8 d as a result of irrigation and insecticide treatment schedules, which prevented an exact 7-d sampling period. The change in aphid numbers calculation represents the change in average number of aphids per leaf (averaged over all three replications for each of the four treatments) per day per week. This value was transformed to Ln to stabilize variances for linear and stepwise regression analyses; before transformation, 0.5 was added to rate of change to eliminate zero and negative values equal to or more than  $-0.4$ . If the change in aphid numbers per week was less than  $-0.4$  during the period before peak (maximum) numbers of aphids per leaf at the end of the season, the value was not used in the regression analyses. Rapid decreases in aphid numbers are thought to be associated with predation (Slosser et al. 1998), but predator numbers were not counted in this study so predator effects could not be included in the regression analyses. As a result of these deletions, a sample size of 103 data points ( $n = 103$ ) was maintained in all regression analyses related to the 4-yr study. The calculations were based on data collected beginning the last week in July and continuing until aphid populations reached peak numbers in September or October.

For linear and stepwise regression analyses, the relationships between average change in aphid numbers each week and the average weekly values for the following independent variables were investigated: number of aphids per leaf; concentration of leaf fructose, glucose, sucrose, total sugars, and starch (micrograms per square centimeter) levels; sugar ratio [(glucose + fructose)/sucrose] and sucrose/glucose; leaf moisture and nitrogen (percentage); total amino acids (micromoles per square centimeter); sucrose:total amino acids and sucrose:nitrogen ratios; hours of sunlight (daylength); daily high temperature ( $^{\circ}\text{C}$ ); and solar radiation (Watts per square meter). The equations were developed by selecting from linear and quadratic functions for each independent variable and from linear multiplicative two-way

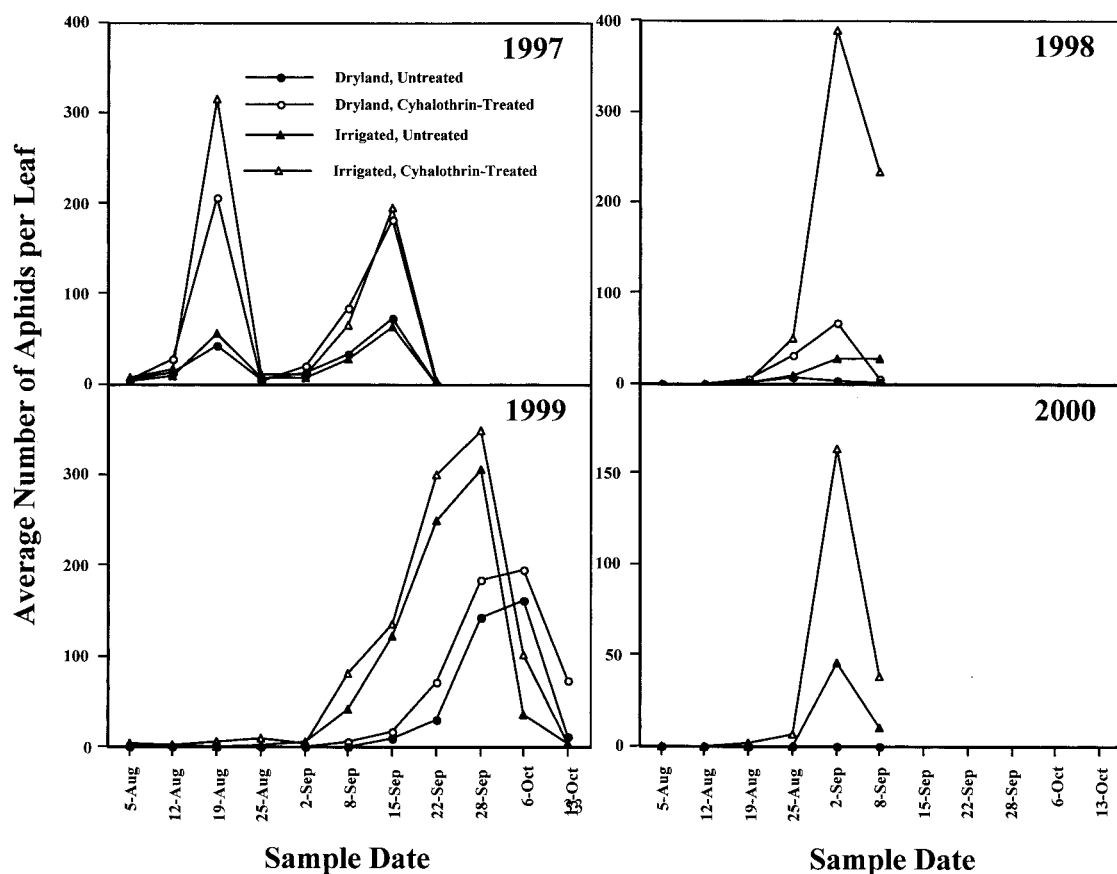


Fig. 1. Cotton aphid population trends from 1997 to 2000 in two irrigation and two spray treatments at Chillicothe, TX. Data for 1997–1999 are from Slosser et al. (2001, 2002).

interactions of the independent variables, particularly between percentage of leaf moisture and percentage of leaf nitrogen and between percentage of leaf moisture and the various sugar concentrations. Several variations in sugar ratios were investigated, but the ratios selected for discussion provided the best correlations with change in aphid numbers. Per the recommendation of Gomez and Gomez (1984), we used treatment means averaged over replications rather than individual replication data for regression.

### Results

Peak aphid numbers per leaf (Fig. 1) occurred on 19 August and again on 15 September 1997, between 25 August and 8 September 1998, between 28 September and 6 October 1999, and between 4 and 12 September 2000. At peak densities, lowest and highest numbers of aphids per leaf occurred in the untreated dryland and  $\lambda$ -cyhalothrin-treated irrigated treatments, respectively. The corresponding numbers ( $\bar{x} \pm \text{SE}$ ) were  $43.5 \pm 9.4$  and  $315.0 \pm 108.2/\text{leaf}$  on 19 August and  $72.7 \pm 16.4$  and  $194.4 \pm 18.0/\text{leaf}$  on 15 September 1997,  $6.4 \pm 5.0$  and  $388.8 \pm 45.0/\text{leaf}$  in 1998,  $161.6 \pm 44.2$  and  $348.8 \pm 21.7/\text{leaf}$  in 1999, and

$0.0 \pm 0.0$  and  $163.0 \pm 49.0/\text{leaf}$  in 2000. There were generally less than five aphids per leaf the first week in August in all treatments each year.

Average maximum and minimum temperatures and total rainfall for June, July, August, September, and October 2000 were  $30.6^\circ\text{C}$ ,  $19.5^\circ\text{C}$ , 6.6 mm;  $36.5^\circ\text{C}$ ,  $21.8^\circ\text{C}$ , 1.0 mm;  $39.1^\circ\text{C}$ ,  $23.3^\circ\text{C}$ , 0.0 mm;  $34.1^\circ\text{C}$ ,  $16.8^\circ\text{C}$ , 0.0 mm, and  $24.6^\circ\text{C}$ ,  $13.0^\circ\text{C}$ , 4.8 mm, respectively. These data are presented here to complete the environmental data set for the 4-yr test; the data for 1997–1999 and long-term (1982–1999) average data were similarly enumerated by Slosser et al. (2001). No rainfall occurred in August and September 2000, and this may be the reason that aphid populations were  $\leq 0.02/\text{leaf}$  during those months in untreated dryland plots. Rainfall was above average and minimum temperatures were below the long-term averages in 1997 and that was the only year that aphid populations reached two peaks, the first during August and the second during September.

An ANOVA (Table 1) indicated that leaf concentrations of fructose, glucose, and sucrose, sugar ratio, and percentage leaf moisture and nitrogen were significantly influenced by year, irrigation treatment, and week, but not by spray treatment. Aphid numbers

Table 1. Source of variation in analysis of variance and associated *F* values for cotton aphid numbers and potential cotton leaf nutritional components (Chillicothe, TX, 1997–2000)

Source of variation	df for <i>F</i>	Fructose conc.	Glucose conc.	Sucrose conc.	Sugar ratio	% Moisture	% Nitrogen <sup>a</sup>	Aphids/leaf
Year (Y)	3, 8	95.20*	60.63*	21.53*	36.95*	78.73*	62.34*	10.42*
Irrigation (I)	1, 8	8.71*	9.30*	46.44*	143.53*	205.57*	133.95*	49.57*
Y × I	3, 8	2.82	0.66	32.71*	54.51*	16.29*	8.53*	9.07*
Spray (S)	1, 16	0.00	0.11	0.01	0.24	0.01	1.39	62.42*
Y × S	3, 16	0.34	0.35	0.12	0.55	0.17	0.54	11.15*
I × S	1, 16	0.49	0.28	0.00	0.01	0.02	0.67	17.93*
Y × I × S	3, 16	0.16	2.05	0.21	0.18	0.07	0.09	5.17*
Week	5, 235	8.78*	14.70*	9.04*	10.69*	48.33*	36.59*	5.52*

An asterisk (\*) denotes significant *F* value ( $P \leq 0.05$ ).

<sup>a</sup> For nitrogen, numerator df = 1 except week-5, and denominator df are one-half of the values shown, except week-115.

were significantly influenced by year, irrigation and spray treatments, and by week.

Regression analyses across all years and treatments indicated that the weekly change in aphid numbers was correlated with number of aphids per leaf, sugar ratio, percentage of leaf moisture, and daily maximum temperature (Table 2, equation 1). There was a positive linear and negative quadratic response to aphid numbers and temperature, and there was a negative linear response to sugar ratio and positive linear response to leaf moisture. Total amino acids and starch were not selected in stepwise regression analyses.

Leaf nitrogen data were not available for the 1997 and 1998 data, so these years were omitted, and an analysis was conducted on the 1999 and 2000 data sets (Table 2, equation 2). In the second equation, the percentage of leaf moisture by percentage of leaf nitrogen interaction replaced leaf moisture in equation 1, and percentage of leaf nitrogen became an additional significant variable in equation 2. In both equations, aphid numbers, plant nutritional factors, and temperature interact to regulate change in aphid numbers.

To determine the role of sugar ratio, the six independent variables in equation 1 (Table 2) were examined using the individual main effects for year (averaged over treatments) and treatment (averaged over years), and the significant independent variables were identified (Table 3). Sugar ratio was not significant in 1997 or 2000, but ratio showed a significant negative influence on change in aphid numbers in 1998 and 1999. Sugar ratio did not significantly influence the change in aphid numbers in either dryland treatment, but the ratio showed a significant negative influence in both irrigated treatments (untreated and cyhalothrin-treated). ANOVA (Table 1) and multiple regression analyses (Table 3) indicate that λ-cyhalothrin did not influence percentage leaf moisture or sugar ratio.

When leaf concentration of glucose + fructose was greater than the concentration of sucrose, sugar ratio was >1, but when concentration of glucose + fructose was less than the concentration of sucrose, sugar ratio was <1. The highest sugar ratios in dryland and irrigated cotton were observed in 1998 and 1999 (Table 4), and sugar ratios were >1 in irrigated treatments in

Table 2. Relationship between change in aphid numbers and plant and abiotic environmental variables (Chillicothe, 1997–2000)

Independent variable ( $x_i$ )	Equation 1 <sup>a</sup> (1997–2000)				Equation 2 <sup>a</sup> (1999–2000)			
	Coefficient	$r^b$	$t$	$P$	Coefficient	$r^b$	$t$	$P$
Constant (a)	−20.379 ± 4.561	—	−4.47	<0.001	−23.544 ± 7.110	—	−3.31	0.002
$x_1$ aphids per leaf	0.029 ± 0.002	0.787	12.51	<0.001	0.031 ± 0.004	0.778	8.75	<0.001
$x_2$ (aphids per leaf) <sup>2</sup>	−5.426 E-05 ± 6.883 E-06	−0.627	−7.88	<0.001	−6.664 E-05 ± 1.074 E-05	−0.660	−6.20	<0.001
$x_3$ sugar ratio	−0.094 ± 0.021	−0.417	−4.49	<0.001	−0.075 ± 0.037	−0.273	−2.01	0.050
$x_4$ moisture	0.025 ± 0.010	0.237	2.39	0.019	—	—	—	—
$x_5$ temperature °C	1.135 ± 0.276	0.387	4.12	<0.001	1.511 ± 0.409	0.463	3.69	0.001
$x_6$ (temperature °C) <sup>2</sup>	−0.017 ± 0.004	−0.402	−4.30	<0.001	−0.022 ± 0.006	−0.470	−3.76	<0.001
$x_7$ % leaf nitrogen	—	—	—	—	−2.116 ± 0.757	−0.368	−2.80	0.007
$x_8$ (% leaf nitrogen × % leaf moisture)	—	—	—	—	0.023 ± 0.008	0.389	2.99	0.004
$R^2$			0.872				0.880	
Adjusted $R^2$			0.864				0.864	
$F^c$			108.65				52.59	
Shapiro–Wilk W			0.985				0.991	
$P$ (W)			0.282				0.943	
Mallow's $C_p$			7.0				8.0	
Durbin–Watson			2.04				2.01	

MSE, mean square error.

<sup>a</sup>  $y = \ln$  of average change in numbers of aphids per leaf per day per week, and  $y = a + bx_1 + \dots + bx_n$ ;  $n = 103$  for equation 1 and  $n = 58$  for equation 2.

<sup>b</sup> Partial correlations are significant ( $P \leq 0.05$ ).

<sup>c</sup> Equation 1, df = 6, 96 and MSE = 0.266 and  $P < 0.001$ ; for equation 2, df = 7, 50, and MSE = 0.266 and  $P < 0.001$ .



Table 3. Significant *t* values for year and treatment main effects in multiple regression analysis for rate of change per day per week for number of aphids per leaf ( $y = \ln$ ) and six independent variables (Chillicothe, TX)

Independent variable ( $X_i$ )	1997	1998	1999	2000	Dryland untreated	Dryland + $\lambda$ -cyhalothrin	Irrigated untreated	Irrigated + $\lambda$ -cyhalothrin
$X_1$ aphids per leaf	7.05	8.73	3.72	11.45	10.13	8.09	7.97	8.58
$X_2$ (aphids per leaf) <sup>2</sup>	-4.02	-6.84	-2.49	-7.70	-7.55	-6.16	-5.55	-5.36
$X_3$ sugar ratio	—	-3.32	-3.65	—	—	—	2.42	-2.67
$X_4$ leaf moisture	—	2.75	2.52	—	—	—	—	—
$X_5$ temperature °C	—	—	4.45	—	—	5.33	—	—
$X_6$ (temperature °C) <sup>2</sup>	—	—	-4.74	—	—	-5.29	—	—
$R^2$	0.859	0.925	0.899	0.962	0.877	0.938	0.846	0.912
Adjusted $R^2$	0.845	0.906	0.879	0.957	0.867	0.927	0.825	0.898
$F$	63.77	48.97	44.68	225.71	85.73	83.41	40.35	65.44
$P$ ( $F$ )	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Shapiro-Wilk $W$	0.961	0.949	0.973	0.865	0.905	0.991	0.957	0.962
$P$ ( $W$ )	0.465	0.326	0.504	0.008	0.018	0.996	0.332	0.501
Mallow's $C_p$	3.0	5.0	7.0	3.0	3.0	5.0	4.0	4.0
$n$	24	21	37	21	27	27	26	23

All values are significant at  $P < 0.025$ ; a dash indicates the independent variable was not significant ( $P > 0.05$ ); the independent variables shown are the same as those in equation 1, Table 2.

three (1998, 1999, and 2000) of the four years. Sugar ratio was  $>1$  in dryland treatments in 1999 only. These data indicate that population growth was limited by high levels of glucose and fructose (sugar ratio  $>1.5$ ) in cotton leaves.

Although leaf moisture and sugar ratio can be considered nutritional factors, both may be directly affected by climatic conditions during a growing season. For example, 1997 was a mild year climatically; percentage of leaf moisture levels was highest and ambient temperatures were lowest of the 4 yr (Table 4). The year 2000 was the most severe climatically with lowest leaf moisture levels and highest ambient temperatures. No rainfall was received in August–September 2000, whereas rainfall was  $>12.7$  cm each month in August–September 1997, and these differences are evident in average leaf moisture values during these 2 yr (Table 4). The role of temperature was not clearly identified in the study (Tables 3 and 4) because temperature records were not taken within the plant canopy, and temperatures in irrigated cotton

would have been cooler compared with temperatures in dryland cotton.

The effect of sugar ratio on rate of weekly change in aphid numbers was influenced by leaf moisture and ambient temperature conditions (Fig. 2). Equation 1 (Table 2) was used to develop the linear relationships between weekly change and sugar ratios varying between 0.2 and 11.2 (data range 0.2–14.8), by using 50 aphids per leaf, which is the treatment threshold during the summer. When sugar ratio was 1.70, weekly change in aphid numbers was 1 under conditions of average leaf moisture (68.8%) and average temperature (37.4°C). When temperatures were high (68.8% leaf moisture, 40.6°C), maximum change in numbers was 0.51 when sugar ratio was 0.20. Weekly change in numbers became negative when sugar ratio was  $>5.20$ . Under the most optimum conditions (78.2% leaf moisture, 31.1°C), weekly change in aphid numbers was 1.05 when sugar ratio was 6.20. When aphid populations are near the treatment threshold of 50 per leaf, these relationships indicate that high levels of sucrose

Table 4. Yearly average ( $\pm$  SE) numbers of aphids, sugar ratios, leaf moisture, and temperature in dryland and irrigated cotton (Chillicothe, TX)

Water treatment	Year of study <sup>a</sup>			
	1997	1998	1999	2000
	Aphids/leaf			
Dryland	38.3 $\pm$ 16.6	9.8 $\pm$ 5.8	0.8 $\pm$ 0.5	0.1 $\pm$ 0.0
Irrigated	44.6 $\pm$ 25.3	61.9 $\pm$ 35.3	13.8 $\pm$ 6.8	22.2 $\pm$ 13.6
	Sugar ratio <sup>b</sup>			
Dryland	0.62 $\pm$ 0.05	0.92 $\pm$ 0.18	2.93 $\pm$ 0.73	0.68 $\pm$ 0.03
Irrigated	0.73 $\pm$ 0.10	1.65 $\pm$ 0.40	5.14 $\pm$ 1.07	1.18 $\pm$ 0.05
	% Leaf moisture			
Dryland	71.9 $\pm$ 0.8	67.3 $\pm$ 1.0	62.8 $\pm$ 0.8	60.0 $\pm$ 0.5
Irrigated	74.7 $\pm$ 0.7	71.5 $\pm$ 0.6	71.3 $\pm$ 0.6	70.6 $\pm$ 0.5
	Ambient maximum temperature (°C)			
—	34.1 $\pm$ 0.5	37.9 $\pm$ 0.4	38.3 $\pm$ 0.3	39.2 $\pm$ 0.2

<sup>a</sup> Data are averaged over the 6-wk period from 4 August to 12 September,  $n = 12$  for each mean, except for temperature,  $n = 6$ .

<sup>b</sup> Sugar ratio is (glucose + fructose concentration/sucrose concentration) in micrograms per square centimeter.

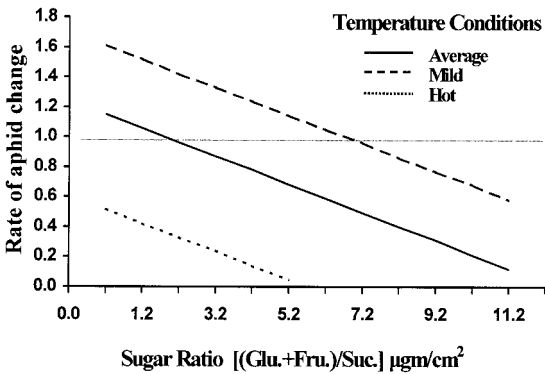


Fig. 2. Change (Ln) in numbers of aphids per leaf per day per week versus sugar ratio, by using 50 aphids per leaf and various ambient temperature and leaf moisture conditions. Refer to equation 1 in Table 2 for equation and to the associated text for actual ambient temperature and leaf moisture conditions used.

(sugar ratio <2) are necessary to maintain a weekly change >0 when environmental conditions are unfavorable (58.1% leaf moisture, 40.6°C), but when the environment is moderate to very favorable, population change remains positive and sugar ratio is not as critical.

Regression analyses indicated that percentage of dark-colored morphs was negatively correlated with daily maximum temperature and hours of daylight, and positively correlated with percentage of leaf moisture and sucrose concentration (Table 5, equation 1). The Durbin-Watson statistic was 1.47, which indicated that random errors around the regression line exhibited positive autocorrelation ( $P = 0.002$ ) and that additional independent variables were needed in the model (Anonymous 2000). An analysis was conducted on the 1999 and 2000 data sets to evaluate the

influence of leaf nitrogen (Table 5, equation 2). Sucrose concentration in equation 1 (Table 5) was replaced by the sucrose to glucose ratio in equation 2 (Table 5), and percentage of leaf nitrogen and the percentage of leaf moisture by percentage of leaf nitrogen interaction became additional significant independent variables in equation 2 (Table 5). The Durbin-Watson statistic was 2.11, indicating that autocorrelation was eliminated in the second equation.

Discussion

Our results indicate that λ-cyhalothrin did not alter the leaf biochemical attributes that we measured (Table 1), including starch ( $F = 0.176$ ;  $df = 1, 16$ ;  $P > 0.05$ ) and total amino acids ( $F = 0.026$ ;  $df = 1, 8$ ;  $P > 0.05$ ). Similarly, Kerns and Gaylor (1993) reported that the pyrethroid cypermethrin did not alter total amino acids. Total sugars (fructose + glucose + sucrose,  $\bar{x} \pm SE$ ) were statistically similar in untreated ( $168.5 \pm 13.1$ ) and λ-cyhalothrin-treated plots ( $165.9 \pm 12.6$ ) ( $F = 0.001$ ;  $df = 1, 16$ ;  $P > 0.05$ ). Thus, our data do not confirm other reports (Dominick and Mohanasundaram 1992, Ravindhran and Xavier 1997) that pyrethroids increased total leaf sugars. We examined plant leaf data obtained within 1 wk of chemical application, but there were no trends indicating an influence of treatment (data not shown).

To evaluate the importance of plant nutrition (leaf moisture and sugar ratio), temperature effects (temperature and temperature<sup>2</sup>) were deleted from equation 1 (Table 2), and the resulting  $r^2$  was 0.838 ( $F = 126.32$ ;  $df = 4, 98$ ;  $P < 0.001$ ). To evaluate the significance of temperature effects, leaf moisture and sugar ratio variables were deleted from equation 1 (Table 2), and the resulting  $r^2$  was 0.840 ( $F = 128.91$ ;  $df = 4, 98$ ;  $P < 0.001$ ). The similar  $r^2$  values indicate that plant nutrition and temperature variables had approxi-

Table 5. Relationship between percentage of dark morph cotton aphids and plant and abiotic environmental variables (Chillicothe, TX, 1997–2000)

Independent variable ( $x_i$ )	Equation 1 <sup>a</sup> (1997–2000)				Equation 2 <sup>a</sup> (1997–2000)			
	Coefficient	$r^b$	$t$	$P$	Coefficient	$r^b$	$t$	$P$
Constant (a)	3.979 ± 0.454	—	8.76	<0.001	−0.005 ± 1.128	—	−0.00	0.997
$x_1$ temperature °C	−0.042 ± 0.006	−0.562	−6.73	<0.001	−0.064 ± 0.006	−0.811	−9.91	<0.001
$x_2$ hours of daylight	−0.265 ± 0.048	−0.489	−5.55	<0.001	−0.231 ± 0.051	−0.539	−4.57	<0.001
$x_3$ moisture	0.017 ± 0.004	−0.426	4.66	<0.001	0.073 ± 0.016	0.544	4.63	<0.001
$x_4$ sucrose concentration	9.845 E-04 ± 5.245 E-04	0.186	1.88	0.064	—	—	—	—
$x_5$ sucrose/glucose ratio	—	—	—	—	0.093 ± 0.025	0.460	3.69	0.001
$x_6$ % leaf nitrogen	—	—	—	—	1.605 ± 0.411	0.480	3.91	<0.001
$x_7$ (% leaf nitrogen × % leaf moisture)	—	—	—	—	−0.021 ± 0.006	0.439	−3.69	0.001
$R^2$			0.749				0.938	
Adjusted $R^2$			0.738				0.930	
$F^c$			72.94				127.49	
Shapiro-Wilk W			0.976				0.990	
$P$ (W)			0.057				0.915	
Mallow's Cp			5.0				7.0	
Durbin-Watson			1.47				2.11	

MSE, Mean square error.  
<sup>a</sup>  $y$  is percentage of dark-colored aphid morphs, and  $y = a + bx_1 + \dots + bx_n$ ;  $n = 103$  for equation 1, and  $n = 58$  for equation 2.  
<sup>b</sup> Partial correlations are significant ( $P \leq 0.05$ ) except for sucrose concentration in equation 1.  
<sup>c</sup> For equation 1,  $df = 4, 98$  and  $MSE = 0.025$  and  $P < 0.001$ ; for equation 2,  $df = 6, 51$  and  $MSE = 0.008$  and  $P < 0.001$ .

mately equal influence on change in aphid numbers. When terms for aphid numbers were omitted from equation 1 (Table 2), the only significant variables remaining were the linear effects for temperature and moisture, and the resulting  $r^2$  was 0.446 ( $F = 40.29$ ;  $df = 2, 100$ ;  $P < 0.001$ ). Average numbers of aphids per leaf apparently were the most important variable affecting change, but both plant nutrition (leaf moisture) and temperature (physical environment) still had a significant influence on change when aphid numbers were omitted from the regression analysis.

The significant independent variables that were identified (Table 2) support earlier findings regarding the importance of temperature, percentage of leaf nitrogen, and the leaf nitrogen by leaf moisture interaction on cotton aphid population dynamics (Slosser et al. 1998). Nevo and Coll (2001) and Cisneros and Godfrey (2001) have reported that adult and nymph densities and intrinsic rate of increase ( $r_m$ ) were positively correlated with increasing levels of nitrogen fertility. The influence of temperature on cotton aphid development and fecundity have been reviewed by Akey and Butler (1989) and Rosenheim et al. (1994) who found that optimal constant temperatures were 25.0–27.5°C.

As indicated in Introduction, there is conflicting information regarding the positive or negative influence of cotton leaf sugar concentrations on cotton aphid populations (Ravindhran and Xavier 1997, Liu and Yang 1993). Simpson et al. (1995) reported that the sucrose to amino acid ratio influenced dry weight growth of the pea aphid. In the analyses reported herein, the sucrose to amino acid and sucrose to percentage of leaf nitrogen ratios did not significantly affect change in aphid numbers ( $t = 0.02$ ,  $P = 0.840$ ;  $t = -0.35$ ,  $P = 0.730$ , respectively). Sugar ratio was the only independent variable in the equations (Table 2) that has not been previously identified as influencing aphid population dynamics.

Aphids feed within phloem sieve tubes (Auclair 1963), and sucrose constitutes >90% of the carbohydrates in cotton phloem sap (Tarczynski et al. 1992). Our samples represented total nonstructural carbohydrates (glucose, fructose, sucrose, and starch) from whole-leaf extracts and not just from phloem. Therefore, our data do not accurately reflect the sugar composition where the aphids actually feed. However, aphid stylet penetration through the leaf may be inter- or intracellular, in which case the aphid would be exposed to higher concentrations of glucose and fructose than occurs in just the phloem. For example, Butler et al. (1972) reported that the percentage of glucose exceeded that of either fructose or sucrose in cotton leaf nectary secretions, which indicates that cotton aphids could encounter high levels of glucose during probing. In their discussion on silverleaf whitefly, *Bemisia argentifolii* (Bellows & Perring), feeding, Freeman et al. (2001) reported that host acceptance is made before the stylets reach the phloem. If the ratio of glucose:fructose:sucrose in leaf tissue sap is not acceptable, the aphid may perceive that the leaf is nutritionally unacceptable and cease to probe and

Table 6. Spearman rank correlations and associated  $P$  values between rate of aphid population change or percentage of dark morphs and associated independent variables (Chillicothe, TX 1999–2000)

Independent variable <sup>a</sup>	Dependent variable			
	Ln Change		% Dark morphs	
	$r$	$P$	$r$	$P$
Aphids per leaf	0.855	<0.001	0.825	<0.001
(Aphids per leaf) <sup>2</sup>	0.855	<0.001	0.825	<0.001
Sugar ratio (glu + fru/suc)	0.373	0.004	0.430	0.001
Sucrose/glucose ratio	-0.531	<0.001	-0.568	<0.001
% Leaf moisture	0.167	0.209	0.156	0.243
Temperature °C	-0.586	<0.001	-0.658	<0.001
(Temperature °C) <sup>2</sup>	-0.586	<0.001	-0.658	<0.001
Hours of daylight	-0.768	<0.001	-0.768	<0.001
% Leaf nitrogen	-0.087	0.513	-0.064	0.632
% Leaf nitrogen × % leaf moisture interaction	0.005	0.970	0.030	0.825

fru, fructose; glu, glucose; suc, sucrose.

<sup>a</sup> Refer to equation 2, Table 2 and equation 2, Table 5;  $n = 58$ .

feed, which in turn would influence change in aphid numbers. This interpretation regarding the negative influence of glucose is supported by the earlier work of Auclair (1967b) who concluded that high concentrations of glucose were detrimental to growth and survival of cotton aphids.

The occurrence of a high percentage of dark-colored morphs is consistently associated with rapid increases in aphid numbers. Rosenheim et al. (1994) reported that the larger sized, dark-colored morphs were more fecund, developed more rapidly, and reproduced earlier during the adult stage than smaller sized yellow morphs. The results shown in equation 2 (Table 5) support the findings of Rosenheim et al. (1994) in that decreasing temperatures and daylengths and increasing levels of leaf nitrogen were associated with an increase in dark morphs. Our results indicate that percentage of leaf moisture and leaf sugar concentrations were additional factors that influenced the percentage of dark-colored aphids. A sucrose to glucose ratio >1 indicated that dark-colored morphs were induced when sucrose concentrations were greater than glucose concentrations in the leaves.

When forced as an additional variable into the regression equation (Table 2, equation 1), percentage of dark morphs was not significant ( $t = -1.08$ ,  $P = 0.281$ ) for predicting weekly change in aphid numbers. Temperature, percentage of leaf nitrogen, the leaf nitrogen by leaf moisture interaction, and an aspect of the glucose and sucrose ratio were significant independent variables in both equations (Tables 2, equation 2, and 5, equation 2). There was a similar relationship between all of the independent variables used in equations 2 (Tables 2 and 5) and change in aphid numbers and percentage of dark morphs, as indicated by the similarities in the Pearson rank correlations (Table 6) between the independent variables and dependent variables. Although dark morphs are associated with the potential for rapid increase in aphid numbers, the proportion of dark morphs in the population does not



define how rapidly the population will increase. For example in the untreated irrigated plots in 1997, aphid numbers reached a peak of  $56.3 \pm 24.3$  ( $\bar{x} \pm \text{SE}$ ) aphids per leaf on 19 August when there were  $22.1 \pm 5.7\%$  dark-colored morphs. Aphid numbers reached a second peak of  $62.6 \pm 22.7$  aphids per leaf on 15 September when there were  $56.0 \pm 11.0\%$  dark morphs. Although declining temperatures and daylengths and other factors influenced production of a higher percentage of dark aphids in September, compared with August, the cooler temperatures and lower leaf moisture, for example, dampened the increase in aphid numbers. Therefore, the nutritional and abiotic environmental variables that interact to regulate the reproductive potential of the individual aphid (induction of dark morphs) are also interacting with other variables to influence the extent to which that potential will be realized.

Kerns and Gaylor (1992) reported that there were significantly more dark aphids on leaf discs treated with sulprofos compared with numbers of dark aphids on leaf discs that were not treated; however, dark aphids were not produced on leaf discs treated with cypermethrin or dicotophos. These workers suggested that gene expression may have been altered by the sulprofos treatment. Percentage of dark morphs was not influenced by  $\lambda$ -cyhalothrin spray treatment ( $F = 2.69$ ;  $\text{df} = 1, 8$ ;  $P > 0.05$ ) or by irrigation treatment ( $F = 0.83$ ;  $\text{df} = 1, 16$ ;  $P > 0.05$ ) in our study.

### Acknowledgments

We thank Bobby Idol (Texas Agricultural Experiment Station, Vernon) for technical assistance. This research was supported by The Texas Agricultural Experiment Station (Project H-8136); USDA-ARS, Western Cotton Research Laboratory; Cotton Incorporated (Projects 97-481 and 97-482), and Texas State Support Committee (Project 98-553TX).

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*Received 8 September 2003; accepted 11 February 2004.*

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